STUDIES ON THE HELMINTH FAUNA OF ALASKA. XVII. NOTES ON THE INTERMEDIATE STAGES OF SOME HELMINTH PARASITES OF THE SEA OTTER

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According to the work of Rausch (1953), two species of helminth parasites, *Porrocaecum decipiens* (Krabbe, 1878) and *Microphallus pirum* (Afanas'ev, 1941), are pathogenic for the sea otter, *Enhydra lutris* (L.), on the Aleutian Island of Amchitka. In continuation of investigations of sea otter mortality on Amchitka during the latter part of May and early June, 1952, the writer made an attempt to obtain information on the life cycles and developmental characteristics of these parasites. It is the purpose of this paper to report the results of these observations.

Materials and Methods

Collections of marine invertebrates were made with special effort to obtain those which are known, from previous studies (Murie, 1940), to be included in the diet of the sea otter. For the most part, these collections were restricted to the intertidal area. Attempts to procure samples of bottom forms in the deeper waters of Constantine Harbor by means of dragging a triangular dredge from the stern of a small collapsible canvas boat were relatively unsuccessful.

Fishes, *Lebius superciliosus* (Pallas) and *Hemilepidotus hemilepidotus* (Tilesius), were obtained from the waters of Constantine Harbor by means of funnel-type fish traps baited with carcasses of birds previously autopsied in connection with related parasite studies. Efforts to obtain the larger species of crabs by the use of crab traps at a depth of about 15 fathoms were unsuccessful. Amphipods, *Ampithoë rubricata* (Montagu) and *Anonyx nugax* (Phipps), were usually abundant on the baits when the traps were pulled for inspection.

With the exception of representative specimens preserved for purposes of identification, most of the marine animals were autopsied in the field.

Trematode metacercariae were placed on a glass slide and excysted by gentle pressure of a cover glass. The excysted larvae were stained *in vivo* with orcein dissolved in acetic acid, by allowing the staining fluid to flow slowly under the cover glass until the desired differentiation was attained. Additional metacercariae which had been removed from the host tissue in the field were counted and preserved in alcohol-formalin-acetic acid (AFA) solution. Supplementary specimens were preserved in AFA, with the metacercariae intact in the host tissue.

Nematode larvae were fixed in AFA and cleared for study in liquefied phenol.

Results

Two species of fishes, a greenling, *L. superciliosus*, and a sculpin, *H. hemilepidotus*, abundant in the waters around Amchitka, were commonly found to contain the larvae of a nematode, *Porrocaecum decipiens*. Observations indicate that

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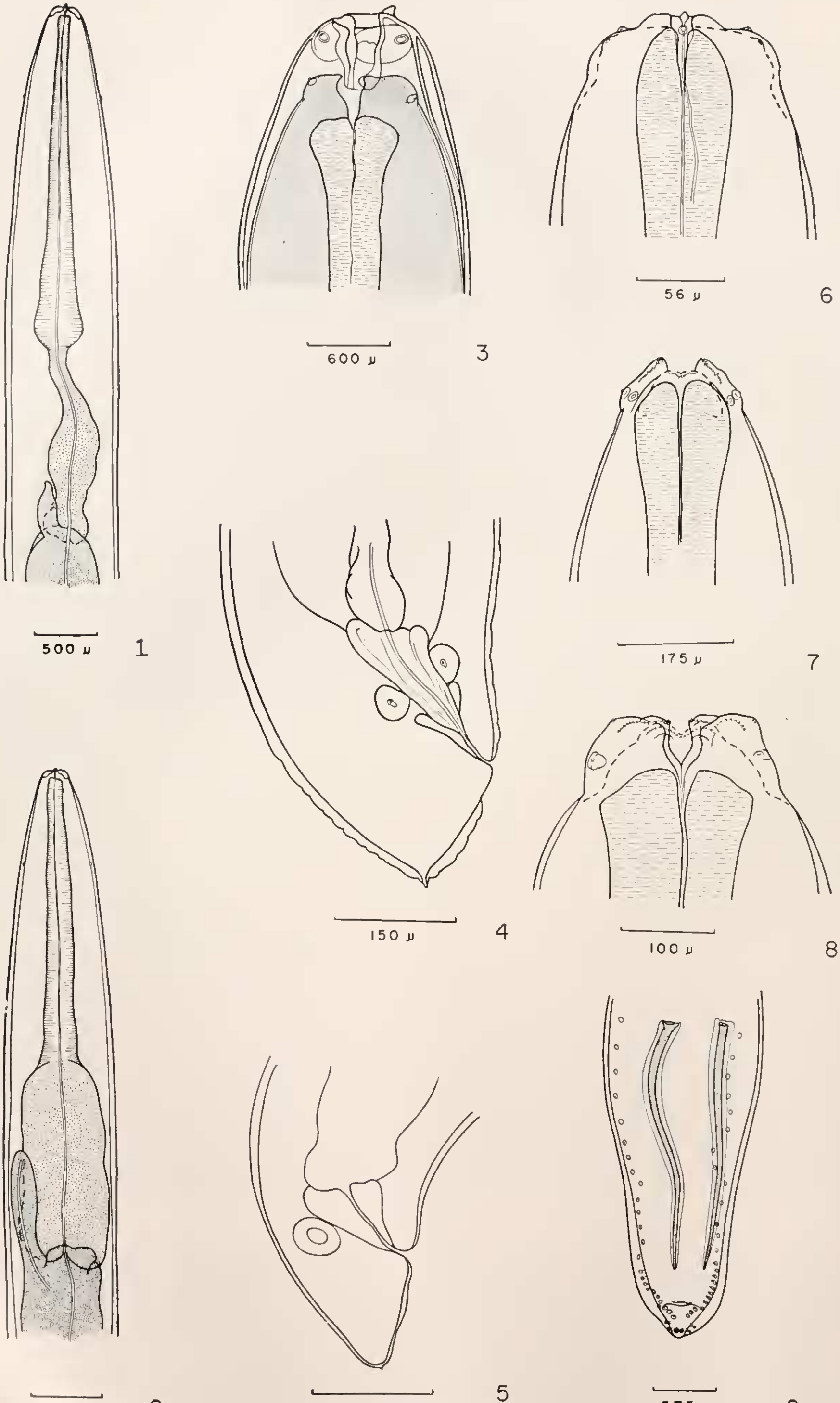
Porrocaecum decipiens (Krabbe, 1878)



Figures 1–9.

the greenling occurs frequently in the diet of the sea otter and probably constitutes the most important source of severe nematode infections acquired by these mammals.

The greenling and sculpin also harbored larval acanthocephalans (*Corynosoma* sp.) which may represent the second intermediate stage of a species parasitic in the sea otter. A brief discussion of this form is included.

The metacercarial stage of the trematode *Microphallus pirum* was found in a hermit crab, *Pagurus hirsutiusculus* (Dana). The finding of the intermediate host for the last larval stage of *M. pirum* permits an understanding of the probable source of the heavy infections with this trematode in the Amchitka sea otter, and will make it possible to obtain additional information on the life cycle and pathogenicity of this species through experimental infections.

The larval stages of *Porrocaecum decipiens* and the metacercaria of *M. pirum* are considered separately in some detail from the standpoint of host occurrence, prevalence of infection, and morphology.

Stiles and Hassall (1899) published a description of *Ascaris decipiens,* to which Baylis (1916) contributed further details. The species was later referred by Baylis (1920) to the genus *Porrocaecum* Railliet and Henry, 1912. Although there appears to be some disagreement concerning the validity of the name *Porrocaecum decipiens*, as indicated by the discussion of the taxonomic status of this nematode given by Johnston and Mawson (1945), the writer has preferred to retain this name for the purposes of this paper.

Several species of marine mammals harbor the adult stage of *P. decipiens*. Around Amchitka, the harbor seal, *Phoca vitulina* L., Steller's sea lion, *Eumetopias jubata* (Schreber), and the sea otter, serve as definitive hosts for this nematode. A list of species from which *P. decipiens* has been recorded in the northern hemisphere was given by Baylis (1937). Several investigators have reported the occurrence of the larval stages in various species of fishes, and it is apparent from these published records that this nematode has an extremely wide geographical distribution.

Although the complete life cycle of *P. decipiens* has never been demonstrated experimentally, Stiles and Hassall (1899) recognized no difference between encysted larvae found in fishes and the youngest worms occurring in the fur seal, *Callorhinus ursinus* (L.). The seal harbored all intermediate stages between the youngest forms and the adults of *P. decipiens*. These authors concluded that such close relationships between the definitive host and the probable intermediate hosts suggested the source of infection nearly to the point of certainty—a view commonly accepted by helminthologists.

FIGURE 1. *Porrocaecum decipiens;* head and esophageal portion of second stage larva from stomach of sea otter. (Earliest larval stage found in this animal.)

FIGURE 2. *P. decipiens;* head and esophageal portion of third stage larva from musculature of *Lebius superciliosus.*

FIGURE 3. *P. decipiens;* head of third stage larva from stomach of sea otter. (In process of shedding cuticular sheath.)

FIGURE 4. *P. decipiens;* tail of third stage larva from musculature of *L. superciliosus.*

FIGURE 5. *P. decipiens;* tail of second stage larva from stomach of sea otter.

FIGURE 6. *P. decipiens;* head of third stage larva from musculature of *L. superciliosus.*

FIGURE 7. *P. decipiens;* head of fourth stage larva from small intestine of sea otter.

FIGURE 8. *P. decipiens;* head of adult male from small intestine of sea otter.

FIGURE 9. *P. decipiens;* tail of adult male from small intestine of sea otter.

According to Stiles and Hassall, both the Alaskan pollock, *Theragra chalcogramma* (Pallas), and the Pacific cod, *Gadus macrocephalus* Tilesius, collected in the Bering Sea, harbored encysted larvae of *P. decipiens*. They considered the former species to be probably the chief source of infection of the fur seal. Scheffer and Slipp (1944) reported *P. decipiens* abundant in the harbor seal from the Pacific coast of the United States. They found the larval stage encysted in the mesentery of *Gadus macrocephalus* in the Aleutian Islands, where the same species of seal was found to be parasitized by the adult worm.

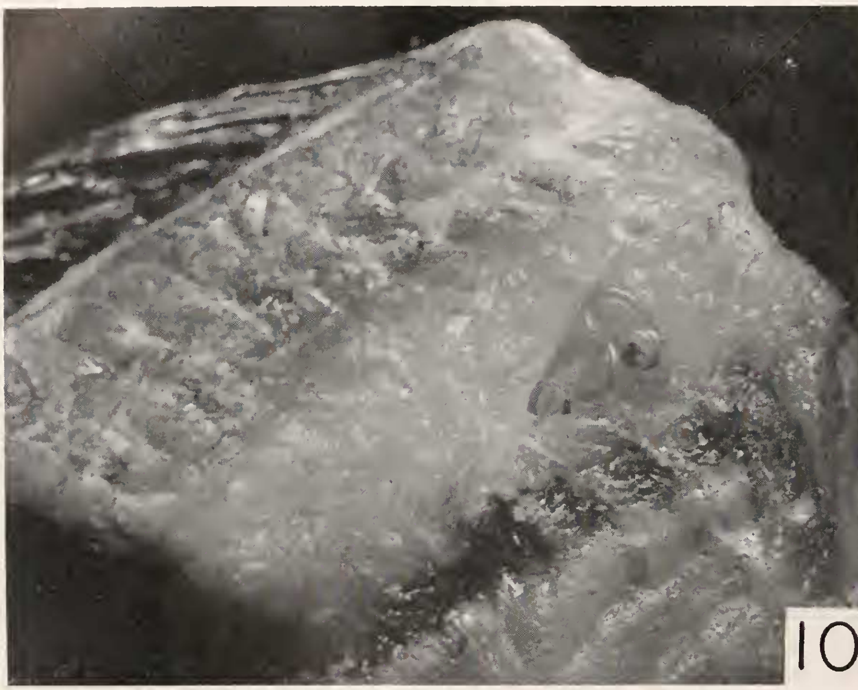


FIGURE 10. Section of dorsal musculature of *L. superciliosus* showing larva of *P. decipiens* in wound cavity.

Rausch (1953) reviewed previous reports of *P. decipiens* in the Aleutian Island sea otter and recorded his observations on the prevalence of the species in the sea otter of Amchitka. His report included an account of the pathological changes in this animal associated with certain developmental stages of *P. decipiens*.

Data: A total of 106 fishes was examined during the present study on Amchitka. These consisted of 75 greenlings, *L. superciliosus*, 15 sculpins, *H. hemilepidotus*, 11 blennies, (Stichaeidae) *Anoplarchus purpurescens* Gill, and 5 tide pool sculpins, *Myoxocephalus niger niger* (Bean). Of these, both *L. superciliosus* and *H. hemilepidotus* were found to contain the larvae of *P. decipiens*. Data concerning these infections are summarized in Table I. Prevalence of infection does not appear to be correlated with either sex or size of the fishes examined.

Morphology: The larval stages of *P. decipiens* from the musculature of *L. superciliosus* ranged in length from 30 to 50 mm. All of these immature worms possessed a boring tooth in the position of the left ventral lip (Fig. 3) and a small conical projection at the tip of the tail (Fig. 4). The exposed part of the boring tooth measured about 15 μ in length by 30 μ in maximum diameter. The terminal projection attained a length of about 17 μ. The dorsal and ventral lips, although visible beneath the cuticular sheath characteristic of this larval stage, were compressed together in such a manner as to obscure the morphological details. Examination of identical specimens from the sea otter revealed that several were in the process of shedding the cuticular sheath (Fig. 3). The boring tooth and terminal projection are lost during this molt. The three characteristic ascarid lips are incompletely developed but appear to be functional as

TABLE I

Prevalence of larval Porrocaecum decipiens according to sex and size of fishes collected at Amchitka

Fish species: Total number examined: Total number infected:	*L. superciliosus* 75 30 (40%)		*H. hemilepidotus* 15 3 (20%)	
Sex	Male	Female	Male	Female
Number of specimens	27	48	10	5
Range in length	210–375 mm.	210–395 mm.	154-345 mm.	170–285 mm.
Average length	292 mm.	319 mm.	251 mm.	248 mm.
Range in weight	101–609 g.	105–960 g.	114–520 g.	57–342 g.
Average weight	336 g.	444 g.	252 g.	230 g.
Numbers infected	10 (37%)	20 (41.5%)	1 (10%)	2 (40%)
Range in numbers of larvae per infected fish	1–9	1–14	1–	1–3
Average number of larvae per infected fish	2.7	2.9	1.0	2.0

soon as the cuticle is shed. The dorsal lip bears two large papillae and each of the ventral lips is provided with one. The excretory organ consists of a single, flattened, band-like cell which extends ventrally, with several lateral branches, through the anterior region of the worm. The excretory pore is located ventrally between the two ventro-lateral lips. The esophagus is divided transversely into an anterior muscular portion and a posterior glandular organ or ventriculus. The digestive tract is well developed and an intestinal diverticulum, directed anteriad, is present in all specimens from the musculature of the greenling. The esophageal region of a typical larva from the musculature of this fish is illustrated in Figure 2. Measurements of pertinent structures are included in Table II.

In comparing larvae from the fish musculature, no differences, except for those of size, were noted. A grouping of these larvae according to length, and their location within the fish musculature, indicates that these differences in size are correlated with growth and development.

There was no evidence of the beginning development of reproductive organs in larvae from the fish musculature.

A study of the immature stages of *P. decipiens* harbored by the sea otter revealed that they are morphologically identical with those found in the musculature of *L. superciliosus.* Some of these still retained their cuticular sheaths, a few were in the process of shedding the cuticle, and others had completed this molt.

Smaller specimens (18 to 30 mm. in length), representing a stage of development earlier than any found in the fish, were also present in the sea otter (Fig. 1). These larvae were usually seen in dense clusters with their anterior ends deeply

TABLE II

Data on morphological details of larval Porrocaecum decipiens grouped according to location of larvae, showing relationship between stages of development and migration through the fish musculature. (Measurements of youngest larvae from stomach of sea otter included for purposes of comparison)

Source of larvae		Youngest larvae from stomach of sea otter.	In musculature next to abdominal wall of fish.	In thick dorsal musculature of fish.	In tail musculature of fish.
Total length		18–30 mm.	30–37 mm.	38–44 mm.	45–50 mm.
Boring tooth and tail spike		Present	Present	Present	Present
Total length of esophagus	Range Average	2.66–4.16 mm. 3.29 mm.	3.29–3.64 mm. 3.41 mm.	3.38–3.85 mm. 3.61 mm.	3.45–4.35 mm. 3.84 mm.
Length of muscular part	Range Average	1.82–3.15 mm. .235 mm.	1.89–2.10 mm. 1.99 mm.	1.93–2.38 mm. 2.15 mm.	2.01–2.80 mm. 2.30 mm.
Length of ventriculus	Range Average	770–1260 μ 946 μ	1.28–1.54 mm. 1.39 mm.	1.43–1.47 mm. 1.45 mm.	1.33–1.86 mm. 1.56 mm.
Length of diverticulum		Absent in larvae 18–28 mm. Beginning in larvae 30 mm.			
	Range Average	112–490 μ 340 μ	700–980 μ 864 μ	756–1048 μ 870 μ	700–1050 μ 885 μ
Distance to cervical papillae	Range Average	392–700 μ 523 μ	588–728 μ 679 μ	700–770 μ 737 μ	700–770 μ 750 μ

imbedded in the mucosa of the stomach, or associated with intestinal perforations (see Rausch, 1953). These larvae closely resembled those from the greenling, although the ventriculus had a shrunken appearance and the diverticulum was absent in all specimens up to 28 mm. in length. An anteriorly-directed structure about 112 μ in length was present in the position of the ventriculus in most larvae 29 mm. long (Fig. 1), however, and its length had increased more than four times (490 μ) by the time the larvae had reached 30 mm. (Fig. 2). This seems to indicate that development of the diverticulum was very rapid during this stage.

Although larvae of a comparable size were not seen in the greenling, it is possible that these smallest forms represent an earlier developmental stage—one occurring in the intestine or abdominal cavity of the fish, prior to invasion of the musculature. Measurements of the pertinent morphological characters in the youngest larvae from the sea otter are included in Table II.

The nematode infections in the sea otter usually comprised all of the immature stages. The pattern of development of these worms, as interpreted from the study of morphological characteristics and location in the intermediate host (fish) and/or in the definitive host (sea otter), is presented below:

First stage larvae: Motile larva in the egg.

Second stage larvae: Larvae up to 28 mm. in length; boring tooth and tail projection present; ventriculus smaller in diameter than posterior third of muscular part of the esophagus; lips incompletely developed; diverticulum absent or only slightly developed; beginning development of reproductive organs not evident (Figs. 1, 5).

Location in intermediate host: Probably in gastrointestinal tract and/or abdominal cavity of fish.
Location in definitive host: Attached in dense clusters to mucosa of stomach in pinnipeds and sea otter; associated with intestinal perforations in the case of the sea otter.

Third stage larvae: Larvae 30 to 50 mm. in length; boring tooth and tail projection may or may not be present; lips incompletely developed but functional when cuticular sheath is shed; ventriculus well developed; diverticulum present, attaining a length of about 4/7 the length of the ventriculus; beginning development of reproductive organs not evident (Figs. 2, 3, 4, 6).

Location in intermediate host: In the musculature of fish (greenling). Larvae possessing cuticular sheath with boring tooth and tail projection.
Location in definitive host: Attached in clusters to mucosa of stomach in pinnipeds and sea otter. Larvae possessing cuticular sheath with boring tooth and tail projection, cuticle being shed, or molt completed.

Fourth stage larvae: Larvae over 50 mm. in length; boring tooth and tail projection absent; lips completely developed, with dentigerous ridges conspicuous; diverticulum well developed and equal or nearly equal to length of ventriculus; beginning development of reproductive organs evident, but worms sexually immature (Fig. 7).

Located in definitive host only: In stomach and intestine of pinnipeds and sea otter.

Adult stage: Males about 78 mm. in length; females about 110 mm. in length. Characteristics of male: total length of esophagus, 4.5 mm., muscular portion, 3.2 mm., ventriculus, 1.2 mm.; diverticulum extends to anterior extremity of ventriculus; spicules equal, 2.2 mm. in length; post-anal tail length, 271 μ; six lateral pairs of post-anal papillae, three pairs near anus and three pairs terminal (Figs. 8, 9). All morphological characters of the adult *P. decipiens* examined in this study conform to descriptions given by Stiles and Hassall (1899) and Baylis (1916).

Located in definitive host only: In small intestine of pinnipeds and sea otter.

Larval migration, development and encapsulation: In considering the life cycle of *P. decipiens,* it is assumed here that the eggs released by the adult worms in the definitive host are passed into the sea and are ingested by the intermediate host (fishes). The larvae apparently are released from the egg, either in the stomach or intestine of the fish, then penetrate the walls of these organs and migrate through the abdominal cavity into the musculature. Kahl (1938) discussed the occurrence of *P. decipiens* larvae in different parts of the body of the fish (stomach, body cavity, and musculature) and presented a detailed account of the process of encapsulation of these larvae within the muscle tissue.

The pattern of migration, development, and encapsulation of the larvae of *P. decipiens* as observed in *L. superciliosus* appears to be essentially the same as that in smelt, *Osmerus epurlanus,* and red perch, *Sebastes norvegicus,* as described by Kahl. Living larvae were recovered from various places throughout the fish musculature, and it was possible to correlate the stage of larval development with the amount of host-tissue reaction and extent to which migration had progressed. The smallest larvae (30 to 37 mm. long) were found lying in an extended position in the muscle tissue adjacent to the abdominal wall. Macroscopically there was no visible evidence of tissue reaction at this location. Slightly larger forms (38 to 44 mm. long) were found deeper in the muscle tissue dorsolateral to the abdominal cavity. Here, also, the larvae were lying in a more or less extended position and there was little, if any, change in the tissue in which they were imbedded. The largest larvae (45 to 50 mm.) were usually found in the dorso-caudal region of the fish. These larvae were usually more or less coiled, and apparently had ceased migrating. The worms imbedded in the form of a loose coil appeared to have evoked moderate cellular changes, visible as cellular infiltration contrasting in color with the adjacent tissue. More tightly coiled individuals were seen within cavities apparently produced by them (Fig. 10). The reaction of the surrounding tissue was more pronounced here and the cavity contained a reddish-brown amorphous substance along with the worm. The degree of tissue reaction probably is correlated with the duration of larval localization. Other larvae occurred in compact coils within thin-walled capsules. Sections through these capsules demonstrated that the capsule membrane is composed of connective tissue; however, the connective tissue formation is not nearly as extensive as that described by Kahl (1938). This last condition represents the most advanced stage in the process of host tissue reaction observed in the greenling, although on two occasions during examination of the sculpins, the characteristic opaque, lenticular capsule containing a dead worm, similar to those described by Martin (cited by Kahl, 1938), was found. The late "wound-cavity stage" or early "encapsulation stage" in the greenling occurred most frequently in the muscle tissue on either side of the pterygiophores of the ventral fin.

It is of interest to note that exposure of any part of the worm during dissection of the fish usually resulted in its becoming very active, freeing itself completely from the surrounding tissue within a few minutes. When a living larva, soon after removal, was placed free upon the musculature and covered with another sizeable piece of the same tissue, it re-entered and completely imbedded itself in the muscle in less than ten minutes. These observations suggest that the method of penetration is mechanical. The connective tissue of the flesh apparently offers little resistance to penetration by these worms, since they are not restricted by the connective tissue septa as observed by Kahl (1938) to be the case in other large species of fishes.

There is disagreement among investigators concerning the role of the fish in the infection of marine mammals by these nematodes. Joyeux and Baer (1934) expressed the opinion that the life cycle could be accomplished perfectly well without this intermediate host, but that it served to accumulate and distribute the larvae. Other authors (Pinter, 1922; Giovannola, 1936; and Fülleborn, 1923; cited by Punt, 1941) regarded the passage of the larvae through the fish as a physiological requisite for completion of larval growth and development. Kahl (1939) was of the opinion that encapsulation of the larva is a method of defense on the part of the intermediate host but is by no means indispensable for the development of the larva. He concluded that larvae of *P. decipiens* in the digestive tract of the intermediate host had already completed the development necessary to permit establishment within the definitive host, following ingestion. This seems to be the case in the sea otter–greenling cycle as well, although establishment of larvae of this developmental stage is not without adverse effect upon the sea otter. Rausch (1953; p. 594) stated that "The earliest stage found in the sea otter (*i.e.,* worms having a cephalic spike) appears to be the most pathogenic. This larval stage was always associated with intestinal perforation and seemed directly responsible for all sea otter deaths known to have resulted from nematode infection." Inasmuch as the development ordinarily attained during migration and localization in the fish has not been completed, these larvae may have a tendency to continue their vigorous migration following ingestion by the definitive host. This might explain, in part, the pathogenicity of such early stage larvae of *P. decipiens* in the sea otter.

Twice during this study, several immature specimens of *P. decipiens,* identical with those found in the flesh of the greenling, were taken from the stomach of the bald eagle, *Haliaëtus leucocephalus* (L.), and on one occasion from the stomach of Baird's cormorant, *Phalacrocorax pelagicus* (Pallas). These worms were intermixed with the stomach contents and were probably ingested with infected fishes. This species is not considered to be parasitic in these birds. Murie *et al.* (unpublished data) reported finding *L. superciliosus* in the nests of the bald eagle on several occasions. Krog (1953) has discussed the occurrence of greenling and other species of fishes in the nests of the bald eagle on Amchitka.

Corynosoma sp.

Most of the greenling and sculpin examined in this work harbored late-stage acanthocephalan larvae of the genus *Corynosoma.* These were found attached to the mesenteries. Rausch (1953) recorded *C. strumosum* (Rudolphi, 1802) in addition to an undescribed species of this genus [2] from both the sea otter and Steller's sea lion at Amchitka. Afanas'ev (1941) described *C. enhydris* from the sea otter of the Komandorskii Islands. It is quite probable that the immature form in the fish is an intermediate stage of one of these species. Immature specimens of

[2] This species has been recently described by Dr. H. J. Van Cleave as *Corynosoma villosum* (J. Parasit., **39**: 1–13. 1953).

this genus, similar to those taken from the fishes, were also found in the small intestine of the bald eagle. It is doubtful that these worms reach maturity in this avian host. A discussion of the status of these worms in the bald eagle has been presented in a previous publication (Schiller, 1952). All acanthocephalan material was studied by the late Dr. H. J. Van Cleave, Department of Zoology, University of Illinois.

Rausch (1953) reviewed the taxonomic status of this species and presented a discussion of the pathological changes in the intestine of the sea otter associated with the presence of this parasite.

Microphallus pirum (Afanas'ev, 1941)

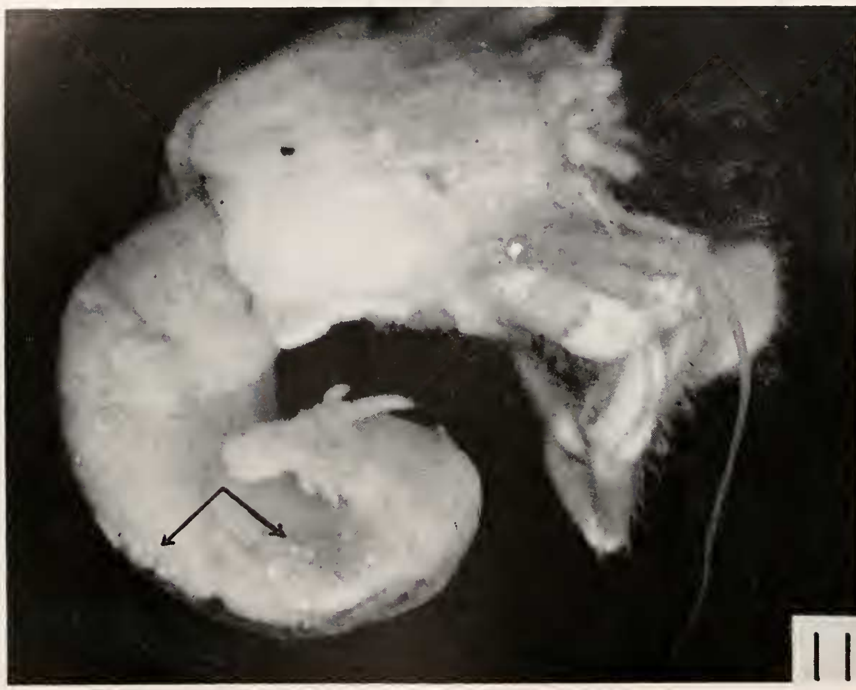
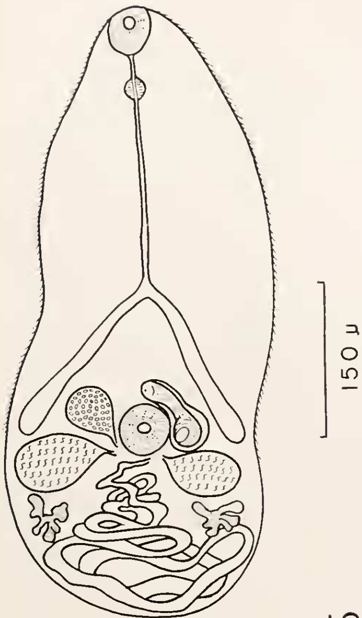


FIGURE 11. *Pagurus hirsutiusculus* (about 3½ ×). Arrows indicate metacercariae of *Microphallus pirum*.

Studies of the life cycle of trematodes of the genus *Microphallus* have been mainly concerned with fresh-water species. A notable exception is the work of Stunkard (1951) with *M. limuli*, whose metacercariae were found in the horse-shoe crab, *Limulus polyphemus*. His work included a critical consideration of the systematic position of the genus *Microphallus*.

During the present study the metacercarial stage of *M. pirum* was found attached rather insecurely to the inner lining of the abdominal wall and to the tissue supporting the viscera of a hermit crab, *P. hirsutiusculus* (Fig. 11). They were usually most numerous at the juncture of the cephalothorax and abdomen, but in heavy infections these cysts occurred throughout the abdomen and occasionally



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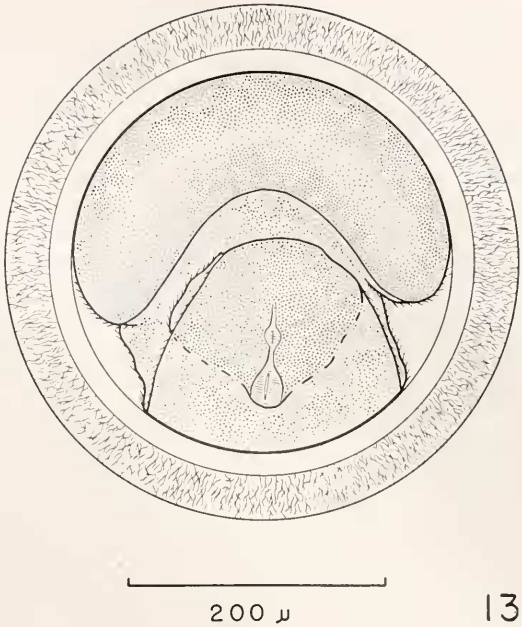

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FIGURE 12. Metacercariae of *M. pirum* from *P. hirsutiusculus* following mechanical excystment.

FIGURE 13. Metacercaria of *M. pirum* from *P. hirsutiusculus* prior to excystment.

FIGURE 14. Metacercaria of *M. pirum* encysted in the hypodermis lining the carapace of *Telmessus* sp. (Average diameter about 300 µ.)

in the thoracic region, where they were attached to the hypodermis lining the carapace.

According to Dr. Fenner A. Chace, Jr., Curator, Division of Marine Invertebrates, U. S. National Museum (personal communication), *P. hirsutiusculus* is one of the most common hermit crabs on the west coast of North America, ranging from the Pribilofs and Aleutians to San Diego, California, and vertically from low tide to a depth of 17 fathoms. It also occurs in Kamchatka and Japan.

The hermit crabs collected at Amchitka were housed in shells of the gastropods *Buccinum baeri* Middendorff and *Thais emarginata* (Deshayes).

Data: Forty-six (90%) of 51 hermit crabs examined in this study were found to contain encysted metacercariae of *M. pirum*. The numbers of cysts in the infected crabs ranged from 11 to 382, with an average of 87. There appeared to be no correlation in the prevalence of infection with either sex or size of these hermit crabs.

Description of the metacercariae: Cyst spherical; varying from 392 to 490 μ in diameter. Cyst wall double: external wall striated and opaque, about 33 μ in thickness. Metacercaria occupies almost all of the space within the cyst. Body of larva curled ventrad upon itself with anterior end innermost and lateral margins of posterior extremity bent over ventral surface as shown in Figure 13. Excysted larvae variable in length, but average about 580 μ. Cuticular spination conspicuous. Digestive tract well developed. Subterminal oral sucker measures 48×42 μ. Prepharynx 6 to 14 μ in length; pharynx about 42×19 μ. Length of esophagus about 240 μ. Ceca 160 μ in diameter. Genital pore located to left and adjacent to posterior margin of acetabulum. Male copulatory papilla about 20 μ in diameter. Seminal vesicle about 77 μ in length. Testes ovoid, about 80 μ long, located near lateral margins just posterior to ends of ceca. Subspherical ovary about 46 μ in diameter, situated between but somewhat anterior to right testis and acetabulum. Deeply lobed vitelline glands, incompletely developed, occur just posterior to testes. Vitelline ducts were not observed. Uterine loops fill body area posterior to acetabulum. The uterus is devoid of eggs.

The reproductive organs are well developed in the metacercaria of *M. pirum* (Fig. 12). Except for the extent of the vitelline glands and the absence of eggs in the uterus, the metacercaria appears to be identical with the adult worm.

The work of several authors (Strandine, 1943; Rausch, 1947; Stunkard, 1951) suggests a considerable degree of morphological variation and a remarkable lack of host specificity in members of the genus *Microphallus*. This may well be the case with *M. pirum*, since a rather wide range in cyst dimensions is seen in this species and since the adult is known to occur in the arctic fox as well as in the sea otter—two hosts phylogenetically not closely related.

The complete life cycle of *M. pirum* is unknown, but because this species is a digenetic trematode, it can be assumed that the first intermediate host is a snail. In view of this, together with the present knowledge of the second intermediate host, the life cycle of this species, in general, is thought to be as follows: The eggs are released by the adult worms in the small intestine of the sea otter and/or arctic fox and are eliminated in the feces. The miracidia gain entrance to the body of a suitable snail in which the subsequent generations of sporocysts, rediae, and cercariae are produced. The cercariae leave the snail and penetrate the body of the second intermediate host, the hermit crab, in which they encyst and develop to the metacercarial stage. Upon ingestion of the infected hermit crab by the sea otter and/or arctic fox, the metacercariae are liberated and attain sexual maturity in the small intestine of the final host.

Stunkard (1953) found the herring gull, *Larus argentatus*, to be the final host of *M. limuli* and considered it very probable, in view of the lack of host specificity among microphallid trematodes, that shore-birds may also serve as natural definitive hosts for this species. Rausch (1953) suggested that *M. pirum* might infect birds. It therefore seems appropriate to note that no infections of *M. pirum* were found in any birds collected at Amchitka by the writer during the present study. These included the following species with the number examined: red-throated loon, *Gavia stellata* (Pontoppidan) (2); Baird's cormorant, *Phalacrocorax pelagicus resplendens* Audubon (1); lesser Canada goose, *Branta canadensis leucopareia* (Brandt) (1); Aleutian teal, *Anas crecca* (L.) [3] (20); lesser scaup, *Aythya affinis* (Eyton) (3); Pacific eider, *Somateria mollissima v-nigra* Gray (4); bald eagle, *Haliaëtus leucocephalus* (L.) (3); black oyster-catcher, *Haematopius bachmani* Audubon (5); lesser yellow-legs, *Totanus flavipes* (Gmelin) (2); Aleutian sandpiper, *Erolia ptilocnemis* (Ridgway) (5); Pacific godwit, *Limosa lapponica baueri* Naumann (1); northern phalarope, *Lobipes lobatus* (L.) (1); parasitic jaeger, *Stercorarius parasiticus* (L.) (3); glaucous-winged gull, *Larus glaucescens* Naumann (2); arctic tern, *Sterna paradisaea* Pontoppidan (1); pigeon guillemot, *Cepphus columba columba* Pallas (1); Aleutian rosy finch, *Leucosticte tephiocatis griseonucha* (Brandt) (2); Pribilof snow bunting, *Plectrophenax nivalis townsendi* Ridgway (2).

The following marine invertebrates were examined, in addition to the hermit crabs, and were found to be negative for larval stages of parasites infecting the Amchitka sea otter: limpet, *Acmaea digitalis* Eschscholtz (15); mussel, *Mytilus edulis* L. (18); anemone, *Actinea* sp. (16); sea urchin, *Strongylocentrotus dröbachiensis* (Müller) (22); snails, *Buccinum picturatum* Dall (19), *B. baeri* Middendorff and *Thais emarginata* (Deshayes) (37); amphipods, *Ampithoë rubricata* (Montagu) (13) and *Anonyx nugax* (Phipps) (33); isopods, *Idothea (Pentidotea) wosnesenskii* (Brandt) and *Ligia pallasii* Brandt (29); barnacles, *Balanus* spp. (24); octopus, *Octopus ?apollyon* Berry (2).

Discussion

Though the percentage of greenlings infected with the larvae of *P. decipiens* at Amchitka is quite high, the number of larvae per infected fish is relatively low—consequently a large number of fishes would have to be consumed by the sea otter to produce the massive infections frequently found in them. This indicates that fishes may be much more important food species for this animal than formerly supposed. Practically all available information concerning feeding habits of the sea otter has been derived from a study of their feces. A young otter, kept in captivity for a short time during this investigation, was fed living greenlings. The flesh and viscera of the fish were consumed, but the more substantial parts of the skeleton were usually discarded. Such feeding habits, if characteristic of sea otter under natural conditions, would explain the scarcity of recognizable fish remains

[3] The cestode parasites of this bird have been reported separately by Schiller (Proc. Helm. Soc. Wash., **20**: 7–12. 1953).

in their feces. According to Murie *et al.* (unpublished data, referring to the report on fishes collected on the 1937 Biological Survey Expedition to the Aleutian Islands) 42 species of fishes were taken in the Aleutian Islands proper. Probably a number of these may also serve as intermediate hosts for *P. decipiens.*

The relatively large number of metacercariae of *M. pirum* occurring in an individual hermit crab, combined with a high prevalence of infection, would seem to assure parasitism in any suitable final host feeding on these crabs. In consideration of the tremendous numbers of worms occurring in some of the infected sea otter at Amchitka (see Rausch, 1953), it is apparent that a great quantity of hermit crabs must be consumed by these animals. This leads to the conclusion that under present conditions at Amchitka, the hermit crab may also be an important species in the diet of the sea otter.

Other species of crabs, remains of which frequently occur in the feces of the sea otter at Amchitka, may afford additional sources of infection with *M. pirum.* Recent examinations of marine crabs collected on Kodiak [4] disclosed that, in addition to *Pagurus hirsutiusculus*, a crab of the genus *Telmessus*, also harbored the metacercariae of *M. pirum.* The metacercariae in the latter were found attached to the hypodermis lining the carapace (Fig. 14).

In addition to ecological relationships favoring a high degree of parasite survival at Amchitka, crowding of the sea otter and their continual occupation of a rather restricted home-range have resulted in a heavy concentration of parasites here. As a consequence, any mortality due to this parasitism in the sea otter may be expected to increase in proportion to the population density and it is conceivable that disease may continue in epizootic proportions until the sea otter population here is greatly reduced. In view of these circumstances, artificial reduction of the population through redistribution and/or harvest of the sea otter as recommended by Rausch (1953) may be the only practical solution.

The writer wishes to take this opportunity to express his appreciation to the individuals whose assistance and cooperation contributed much to this work. Identification of material was made by the following: Dr. H. Friedmann, Curator, Division of Birds, U. S. National Museum (birds); Mr. Vladimir Walters, Department of Biology, New York University (fishes); Dr. S. S. Berry, U. S. National Museum (octopus); Dr. Fenner A. Chace, Jr., Curator, Division of Marine Invertebrates, U. S. National Museum (hermit crab); Dr. Harald A. Rehder, Curator, Division of Mollusks, U. S. National Museum (mollusks); Dr. Robert Menzies, Scripps Institution of Oceanography, La Jolla, California (isopods); and Mr. C. R. Shoemaker, U. S. National Museum (amphipods).

The U. S. Fish and Wildlife Service supported the cost of the field work on Amchitka and the Military Air Transport Service provided transportation to and from Amchitka.

Summary

1. Two species of fishes, *Lebius superciliosus* and *Hemilepidotus hemilepidotus,* serve as the intermediate host for *Porrocaecum decipiens.* Observations indicate that *L. superciliosus* is the most important source of the nematode infections acquired by the sea otter on the Aleutian Island of Amchitka.

[4] The field work on Kodiak was undertaken by Dr. R. Rausch and Miss R. V. Sacressen of this laboratory.

2. The morphological characteristics of the developmental stages of *P. decipiens* from fish and the sea otter are described.

3. A hermit crab, *Pagurus hirsutiusculus*, has been found to harbor the metacercariae of *Microphallus pirum*, an important parasite of the sea otter at Amchitka, and this larval stage is described.

4. Some ecological relationships which favor a high degree of parasite survival at Amchitka are discussed.

LITERATURE CITED

AFANAS'EV, V. P., 1941. Parazitofauna promyslovykh mlekopitaiushchikh Komandorskikh Ostrovov. *Uchenie Zapiski, Seriia biologischeskikh Nauk.*, **18**: 93–117.

BAYLIS, H. A., 1916. Some ascarids in the British Museum. *Parasit.*, **8**: 360–378.

BAYLIS, H. A., 1920. On the classification of the Ascaridae. I. The systematic value of certain characters of the alimentary canal. *Parasit.*, **12**: 253–264.

BAYLIS, H. A., 1937. On the ascarids parasitic in seals, with special reference to the genus *Contracaecum*. *Parasit.*, **29**: 121–130.

JOHNSTON, T. H., AND PATRICIA M. MAWSON, 1945. Parasitic nematodes. *In* B.A.N.Z. Antarctic Research Expedition 1929–1931. Reports—Ser. B. Pt. 2, **5**: 77–159.

JOYEUX, C. H., AND J. G. BAER, 1934. Les hôtes d'attente dans le cycle évolutif des Helminthes. *Biol. Méd. Paris*, **24**: 482–506.

KAHL, W., 1938. Nematoden im Seefischen. I. Erhebungen über die durch Larven von *Porrocaecum decipiens* Krabbe in Fischwirten hervorgerufenen geweblichen Veränderungen und Kapselbildungen. *Zeitschr. f. Parasitenk.*, **10**: 415–431.

KAHL, W., 1939. Nematoden im Seefischen. III. Statistiche Erhebungen über den Nematodenbefall von Seefischen. *Zeitschr. f. Parasitenk.*, **11**: 16–41.

KROG, J., 1953. Notes and observations of birds on Amchitka Island, Alaska. *Condor* **55**: 299–304.

MURIE, O. J., 1940. Notes on the sea otter. *J. Mammal.*, **21**: 119–131.

PUNT, A., 1941. Recherches sur quelques nématodes parasites de poissons de la mer du Nord. *Nêm. du Mus. D'Hist. Nat. de Belgique, No. 98*, p. 1–110.

RAUSCH, R., 1947. Some observations on the host relationships of *Microphallus opacus* (Ward, 1894) (Trematoda: Microphallidae). *Trans. Amer. Micr. Soc.*, **66**: 59–63.

RAUSCH, R., 1953. Studies on the helminth fauna of Alaska. XIII. Disease in the sea otter, with special reference to helminth parasites. *Ecology*, **34**: 584–604.

RAUSCH, R., AND BETTY LOCKER, 1951. Studies on the helminth fauna of Alaska. II. On some helminths parasitic in the sea otter, *Enhydra lutris* (L.). *Proc. Helm. Soc. Wash.*, **18**: 77–81.

SCHEFFER, V. B., AND J. W. SLIPP, 1944. The harbour seal in Washington State. *Amer. Mid. Nat.*, **34**: 373–416.

SCHILLER, E. L., 1952. Studies on the helminth fauna of Alaska. V. Notes on Adak rats (*Rattus norvegicus* Berkenhout) with special reference to helminth parasites. *J. Mammal.*, **33**: 38–49.

SCHILLER, E. L., 1953. Studies on the helminth fauna of Alaska. XIV. Some cestode parasites of the Aleutian teal (*Anas crecca* L.) with the description of *Diorchis longiovum* n. sp. *Proc. Helm. Soc. Wash.*, **20**: 7–12.

STILES, CH. W., AND A. HASSALL, 1899. Internal parasites of the fur seal. *In* D. S. Jordan. The fur seals and fur-seal islands of the North Pacific Ocean. *Rept. of Fur-Seal Invest. 1896–1897, Pt. 3, 1899.* U. S. Govt. Ptg. Off., Washington, D. C., p. 99–177.

STRANDINE, E. J., 1943. Variation in *Microphallus*, a genus of trematodes, from fishes of Lake Lelanau, Michigan. *Trans. Amer. Micr. Soc.*, **62**: 293–300.

STUNKARD, H. W., 1951. Observations on the morphology and life-history of *Microphallus limuli* n. sp. (Trematoda: Microphallidae). *Biol. Bull.*, **101**: 307–318.

STUNKARD, H. W., 1953. Natural hosts of *Microphallus limuli* Stunkard, 1951. *J. Parasit.*, **39**: 225.